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THE SEGMENTATION OF THE ABDOMEN OF THE HONEYBEE (Apis mellifica L.).

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The determination of the number of segments represented in the insect body has proved sufficiently interesting to attract the attention of a considerable number of morphologists. In this field the segmentation of the head has been the more perplexing part of the problem as well as the more difficult, in contrast with the segmentation of the trunk. The latter, however, has the advantage of being capable of a reasonably certain solution. The earlier workers in this field regarded the trunk of the insect as consisting of ten, or in some cases, of eleven segments. The tenth or eleventh segment, recognized as in most respects comparable to those anterior to it, was regarded as constituting the terminal or end segment, bearing the anal opening. For instance, in *Hylotoma* the eleventh segment bears appendages and possesses a neuromere (Graber 1890) and in *Xiphidium* this segment also bears a pair of appendages, the cerci (Wheeler 1893). Heymons (1895, 1895a), paid especial attention to this problem and introduced the conception, now generally accepted, of a terminal segment or telson—stated to be especially evident in *Gryllotalpa*—comparable to the telson of the *Crustacea*, containing the anus but differing from the other segments in not having paired appendages or other strictly metameric organs. In addition to the appendages of the eleventh segment Heymons found in *Phyllodromia* well defined cœlomic sacs in this segment. In later papers (1896, 1897), Heymons has elaborated this conception, finding plain

evidence of twelve segments in representatives of the *Odonata*, and *Ephemeridæ*, and also in *Lepisma* and other representatives of the *Apterygota*.

This subject has since received but little attention. Carriere and Bürger (1897) state that the abdomen of embryos of the mason bee is composed of ten segments and a telson (p. 330). Further on it is said that eleven pairs of ganglia are present in the abdomen of embryos (p. 368). The latter statement is probably from the pen of Bürger, and clearly indicates the presence of eleven true segments in addition to the telson. This is also seen in the figures. Hirschler (1909) reports finding in *Donacia* "20 Körpersegmente (eventuell 21, wenn wir aus theoretischen Grunden das 12 Abdominalsegment zurechnen)." His figures—especially figures 62 and 64—show clearly eleven abdominal segments in addition to the hypothetical telson.

In the honeybee Bütschli (1870), in one of the earliest accounts of the embryology of this insect, expressly states that there are 17 pairs of ganglia in the ventral chain, and clearly shows three ganglionic swellings in the terminal ganglion in his figure 40. This observation has apparently been overlooked by all subsequent writers on this subject. For example, Grassi (1884), the next investigator after Bütschli to study the embryology of the honeybee, states that the ganglionic chain in the trunk consists of only 13 ganglia.

The writer (1915) reported finding eleven segments bearing neuromeres in the abdomen of embryos of the honeybee and gave figures of the posterior end of embryos showing the development of this part of the ventral chain. Ten pairs of ganglia and the rudiments of the eleventh pair are formed in the abdomen, the 9th, 10th and rudimentary 11th pairs uniting to form a compound ganglion. The evidence was in this instance rather briefly presented and in fact on review appeared rather unsatisfactory. For this reason it appeared to be desirable to present the evidence in a more complete form and also to add some observations regarding the conditions obtaining in larvæ.

At about the stage designated X by the writer (1915), when the rudiments of the antennæ and gnathal appendages are well formed and the development of the organ systems is well under way, sagittal sections, either optical or actual, clearly show that the abdomen is divided into eleven segments, in each of which is a neuromere, representing a pair of ganglia. A few hours

later, at Stage XII, the ventral nerve cord becomes split off from the hypodermis. The 9th, 10th and 11th abdominal segments are now very distinct (text Fig. 1A) and are also shorter than the rest. In these segments the ganglia are still in intimate contact with the hypodermis. Shortly afterwards the separation of the nerve cord is completed and the three pairs of

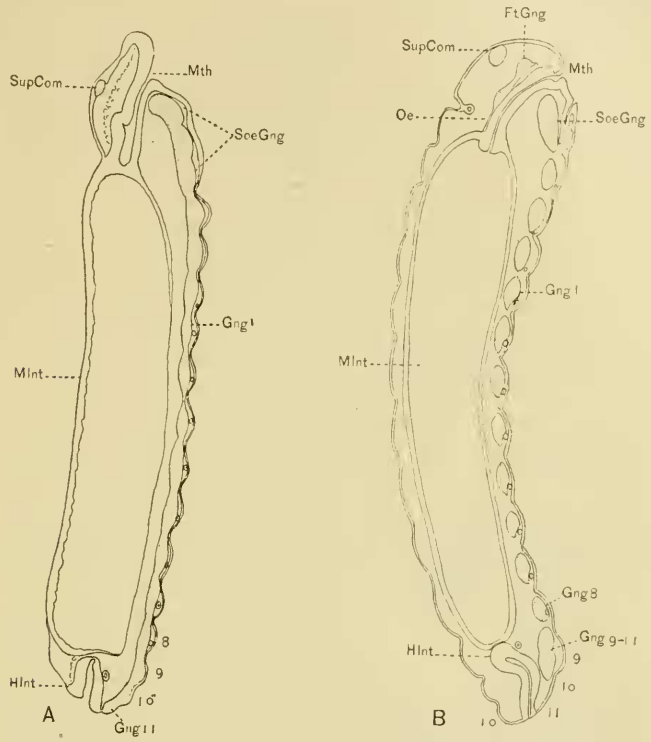


Fig. 1. *A*—Sagittal section through an embryo of Stage XIII. *B*—Sagittal section through recently hatched larva. Nervous system stippled. other organs shown in outline only. *FtGng*, frontal ganglion; *Gng 1–11*, abdominal ganglia 1–11; *HInt*, hind-intestine; *MInt*, mid-intestine; *Mth*, mouth; *Oe*, oesoph-agus; *SoeGng*, suboesophageal ganglion; *SupCom*, supraoesophageal commissure. Abdominal segments indicated by numerals. From camera drawings.

ganglia belonging to these segments appear as a compound ganglion consisting of two evident pairs of simple ganglia equipped with double transverse commissures (indicated in the figures by a lighter shade) and the rudiment of a third pair (Pl. p. 6, Fig. 1). The limits between abdominal segments 9, 10 and 11 are still well defined. Shortly afterward, when the larva has emerged from the egg, the boundaries between the 10th

and 11th abdominal segments can no longer be determined with certainty (text Fig. 1B and Fig. 2). The terminal compound ganglion (*Gng 9-11*) has become shorter and thicker and now lies almost entirely in the 9th abdominal segment. This displacement is due to a lengthening of the trunk and not to an actual shortening of the nerve chain.

The formation of a ganglion—or pair of ganglia—in the 11th abdominal segment also occurs in *Lepisma* (Heymons 1897), *Gryllotalpa*, *Periplaneta*, *Gryllus* (Heymons 1895), *Odonata* and *Ephemerida* (Heymons 1896), *Leptinotarsa* (Doryphora) (Wheeler 1889), *Donacia* (Hirschler 1909), *Hylotoma* (Graber 1890) and *Chalicodoma* (Carriere and Bürger 1898). The fusion of the terminal ganglia of the ventral cord to form a compound ganglion is apparently general among insects. The number of ganglia thus united varies, but appears in young larvæ to be usually three or four, more frequently the latter number. Of the forms above listed, the Ephemerida, as well as embryos of *Hylotoma* and *Chalicodoma* agree with the young honeybee larva in having a terminal ganglion made up of three ganglia. In all cases in which a ganglion rudiment is formed in the 11th abdominal segment this rudiment is distinctly smaller than the others and very usually forms only a vestigial, or at least much reduced ganglion, as in the honeybee. Hirschler (1909) makes the suggestion that in those species of Coleoptera, such as *Hydrophilus*, in which the ganglion of the 11th abdominal segment has not been observed, this ganglion rudiment has suffered reduction to the point of disappearing altogether. This assumption may of course be extended to other insects than those of the order Coleoptera, such as *Forficula*, in which Heymons (1895) could find no neuromere in the 11th abdominal segment.

At the time of hatching, the dorsal hypodermis shows no evidence of an eleventh abdominal segment, only ten of these being indicated by constrictions (text Fig. 1B). Since the formation of the dorsal hypodermis is completed only shortly prior to hatching, it seems reasonable to conclude that only the sternal part of the eleventh abdominal segment is present. This, as is sufficiently evident, unites with the sternal part of the 10th segment. A similar condition obtains according to Heymons (1896) in the true Orthoptera, the *Plecoptera* and some *Odonata* (imagines), the tergum of the 11th abdominal segment being absent in these forms.

The presence of a telson or anal segment in insects seems to be well established on the evidence afforded by the Odonata and Ephemerida, as well as on theoretical grounds (Heymons 1896). The abdomen of the honeybee may therefore be considered as consisting of 12 segments. There is, however, in the honeybee embryo some direct evidence indicating the presence

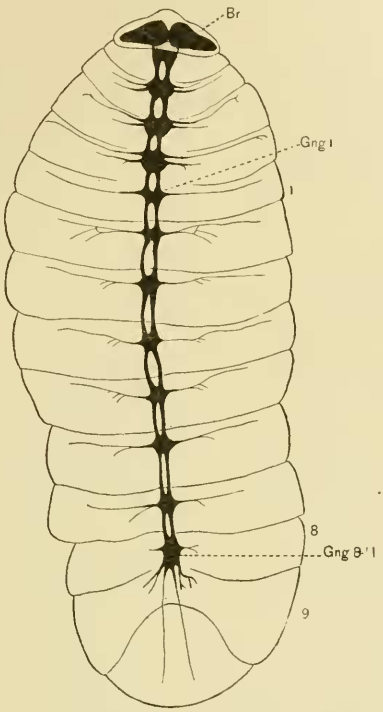
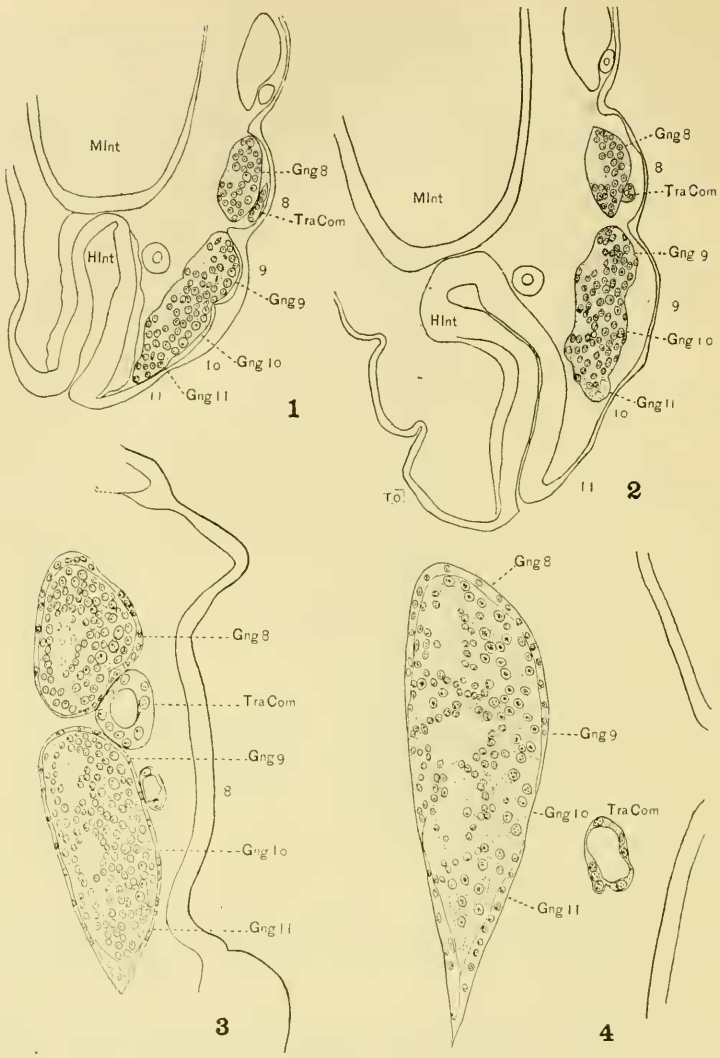


Fig. 2. Nervous system of mature larva. *Br*, brain; *Gng 1–11*, abdominal ganglia 1–11. Abdominal segments indicated by numerals. From camera drawing of a dissection.

of an anal segment. At Stage XII (text Fig. 1A) the ventral hypodermis just cephalad of the proctodæum is indented internally by a deep notch or transverse groove, internally by a shallower one, directly opposite to one another and reducing the intervening hypodermis to one layer of cells. These notches may readily be interpreted as corresponding to intersegmental constrictions and therefore as marking the limits between the 11th abdominal and anal segments. Vestiges of this separation are also to be seen in later stages, but disappear by the time embryonic development is completed.



Explanation of Plate.

Fig. 1. Sagittal section through the posterior end of an embryo of Stage XII. × 260.

Fig. 2. Sagittal section through the posterior end of a recently hatched larva. × 260.

Fig. 3. Sagittal section through the 8th abdominal and terminal ganglia of a larva three days old. × 260.

Fig. 4. Sagittal section through the terminal ganglion of a mature larva. × 260.

Abbreviations: *Gng 8–11*—abdominal ganglia 8–11; *H Int*—hind-intestine; *M Int*—mid-intestine; *TraCom*—tracheal commissure of the 8th abdomnal segment. Abdominal segments indicated by numerals.

As already stated, the ventral nerve cord of the young bee larva consists, in addition to the subœsophageal ganglion, of eleven single (paired) ganglia, and a terminal ganglion composed of three ganglia, the third being much reduced. In mature or nearly mature larvæ (4–5 days old) the ventral nerve chain contains only ten single ganglia and one elongate terminal ganglion situated in the 8th abdominal segment instead of the 9th, as in young larvæ (text Fig. 2). Longitudinal sections through this ganglion show that it is made up of four ganglia, the 8th, 9th and 10th and rudimentary 11th abdominal ganglia (Fig. 4). This ganglion has now a very compact structure, the transverse commissures of the 9th and 10th abdominal segments being brought close together. Sections through younger larvæ of different ages show that the incorporation of the 8th abdominal ganglion into the compound terminal ganglion takes place slowly, being preceded by a gradual approximation of the 8th and the terminal ganglia extending over almost the entire larval period. As the larva increases in size the 8th and 9th (terminal) abdominal ganglia move up into the 8th abdominal segment, as shown in Figure 3, which represents a section through the last two ganglia of a larva three days old. This cephalad migration indicates a relative shortening of the entire ventral nerve cord, probably caused by the evident failure of the nervous system to keep pace with the rest of the larva in respect to increase in size. The terminal ganglion of an old larva possesses four pairs of lateral nerves, the first two having a common root, innervating the 8th abdominal segment while the other two pairs innervate the 9th and 10th abdominal segments and are referable to the ganglia originating in these segments.

The fusion of the four last ganglia of the ventral nerve cord in the larva evidently foreshadows the imaginal condition, although there is no further union of ganglia during the larval period. The composition of the ventral cord in the young larva, the mature larva and the imago may be expressed in the following formulæ, the ganglia of the thoracic segments being indicated by Roman, the abdominal by Arabic numerals, and the ganglia united together to form compound ganglia being enclosed by brackets:

Newly hatched larva..I, II, III, 1, 2, 3, 4, 5, 6, 7, 8, [9, 10, 11].
Mature larva.....I, II, III, 1, 2, 3, 4, 5, 6, 7, [8, 9, 10, 11].
Imago (Snodgrass 1910).I, [II, III, 1, 2], 3, 4, 5, [6, 7], [8, 9, 10, 11].

SUMMARY.

1. The embryos of the honeybee afford plain evidence of the presence of 12 segments in the abdomen, (assuming the presence of a telson), the 11th abdominal segment being represented by its sternite and by the rudiment of a pair of ganglia.

2. In newly hatched larvæ the last three abdominal ganglia, including the rudimentary 11th abdominal, unite to form a compound ganglion situated in the 9th abdominal segment. As the larva grows older the compound terminal ganglion and the ganglion of the 8th abdominal segment move closer together and both come to lie in this segment. In mature larvæ (4–5 days old) the ganglion of the 8th abdominal segment finally becomes incorporated in the terminal compound ganglion, which has then the same composition, as regards number of ganglia, as the terminal ganglion in the imaginal ventral nerve cord.

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